THE BIGAMIC GENERATIONS OF ANDRICUS CORRUPTRIX SCHLECHTENDAL AND ANDRICUS LIGNICOLUS HARTIG (HYMENOPTERA, CYNIPIDAE)

Part II

BY

W. M. DOCTERS VAN LEEUWEN

Leersum

AND

Mrs. J. M. DEKHUIJZEN-MAASLAND

Renkum

INTRODUCTION

In the preceding article[1] on this subject by the first author he reported that the agamic *corruptrix* and *lignicolus* wasps oviposited in the buds of *Quercus cerris* in the summer of 1954. Small pointed galls developed in the infected buds, only the upper half projecting from the bud scales. This bud-gall was new and was therefore described.

Owing to lack of material it was impossible to repeat the breeding experiments in the summer of 1955. Therefore it remained an open question whether the bigamic generation which developed in these new bud-galls belonged to *corruptrix* or *lignicolus*. It might be that the bigamic generations of both wasps inhabited the same bud-gall.

In the summer of 1956 we had ample material at our disposal. In the garden of the former author at Leersum there is one single young tree of the Turkish oak. In order to avoid the possibility that the two wasps would get mixed up we decided that the experiments with the *corruptrix* wasps were to be held in Leersum as the *lignicolus* galls did not occur in this garden. The second author was to experiment on the *lignicolus* wasps in Amsterdam. In the Hortus Botanicus she had at her disposal one specimen of *Quercus cerris* and a few young specimens of *Quercus robur*.

At Leersum in the spring of 1957 we found only the small pointed galls developing from the infected buds. They contained the bigamic generation of *Andricus corruptrix*.

Bud-galls were also found on the Turkish oak in Amsterdam.These, however, were not pointed, but rounded and usually they were clustered together in the bud. These galls contain the bigamic generation of *Andricus lignicolus*. This gall is identical with the bud-gall described as early as 1870 by GUSTAV MAYR of *Andricus circulans* which contained the bigamic generation of *Andricus kollari*.

We bred these bigamic wasps from the two bud-galls further on *Quercus robur*. At Leersum we had the gall of *Andricus corruptrix* and in Amsterdam that of *lignicolus*.

The results of these experiments and the conclusions which may be drawn from them will be described below.

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[1] *Tijdschrift v. Entomologie,* 1956, vol. 98, p. 251—256.

The photographs for the plate were made by Mr. J. VUIJK, in the Botanical Laboratory of Amsterdam. We gladly offer our thanks for his interest and help.

THE WASPS

The wasps of the agamic generations of *Andricus corruptrix, kollari* and *lignicolus* are fairly robust, glossy brown insects. The galls of these three species can clearly be distinguished one from the other, but the same does not hold good for the wasps, see RIEDEL (1910, p. 36). There is some difference in size, the *corruptrix* wasps are the smallest, the *kollari* wasps the biggest, but the difference can only be discerned when a great number of insects are compared. They also emerge at different times; *lignicolus* appears in the Netherlands in July, *corruptrix* in August, while most *kollari* wasps come out in September.

The wasps of the bigamic generations of these three species are small and black. The *circulans* wasp (the bigamic generation of *Andricus kollari*) has been described by MAYR (1870, p. 31), and somewhat more detailed by DALLA TORRE & KIEFFER (1910, p. 479). The bigamic *corruptrix* and *lignicolus* wasps bred by us cannot be discerned morphologically from the *circulans* wasps. The galls of the bigamic wasps of *kollari* and *lignicolus* are identical; the gall of the bigamic generation of *corruptrix* is different: a small pointed bud-gall, see the description.

Consequently it is superfluous to give the morphological descriptions of the wasps of the two new bigamic generations as they would only be exactly the same as the description of the *circulans* wasp. The wasps are about 2 mm long. All the insects are winged.

We suggest calling the bigamic wasps belonging to *Andricus corruptrix* by the name **larshemi** forma nova. Larshem is the name of Leersum in far-off days and it is the place where the first specimens of this wasp were bred.

Further we suggest calling the bigamic wasps belonging to *Andricus lignicolus* by the name **vanheurni** forma nova, after Mr. W. C. VAN HEURN at Wilp near Deventer who has been so helpful all through the investigation.

The material of the wasps is kept in the Zoological Museum, Division of Entomology, in Amsterdam. The galls have been included in the gall herbarium of the first author at Leersum; after his death they will be incorporated in the Rijksherbarium in Leiden.

THE LIFE-CYCLE OF *Andricus corruptrix*

The gall of the agamic generation has been known for quite a long time as occurring in Southern Europe. It was found for the first time in the Netherlands in 1954. The first article contains two pictures of this gall. As it is very difficult to describe it, because its appearance is very variable, we thought best to add two more photographs of this gall which can be found on plate 3 fig. 1 and 2. It shows clearly that the small, obtuse appendages are often very short, while sometimes they are quite absent. The warty, dark spot is always present, but it is not very clear in the pictures. Like the *kollari* gall the *corruptrix* gall does not develop from the bud, but immediately beneath it. The bud remains small, it does not come out, but between the gall and the twig it is flattened more or less, see plate 3 fig. 2, bottom left. The exit opening is situated on one side, somewhere in the middle, see plate 3 fig. 1.

In 1954 the wasps emerged from the galls between August 5 and 10, in 1955 between August 6 and 12, while in 1956, which was a year with a wet and cold summer, the wasps came forth between August 9 and 18. We may therefore conclude that in the Netherlands the agamic *corruptrix* wasps leave their galls in the first half of August. The young galls become visible early in August and are full-grown in September. Some larvae stay a second winter and thus come out after two years. It may be that some specimens stay even longer in the galls, but we have not checked this.

In the garden of the former author there is a tree of *Quercus cerris* about 6 m high. Six robust branches with many one year old twigs were sleeved and in each bag 4 to 6 *corruptrix* wasps were let loose. After two weeks the bags were removed.

On March 20th a small one year old branch was chosen at random from the sleeved branches, broken off and put into a jar in the window in a warm room. After some days the not-infected buds came out and the tops of young leaves came forth. On March 28th the twig bore the first gall of the bigamic generation. This proved that the breeding experiment at any rate had developed according to plan.

It was the new bud-gall which has been described and reproduced in the first article. In this one you will find two more pictures of this gall on plate 3 fig. 3 and 4, the galls being three times their natural size.

Owing to a printing error the first article contains a mistake as to the size of the galls. The right size is: from 2 to 2½ mm long and from 1 to 1½ mm thick. This gall is a real bud-gall, usually there is only one gall in each bud, occasionally there are two. The basal half of the gall is hidden from view owing to the only slightly receding bud-scales, while the distal part of the gall projects outside the scales. The galls end in a point, so that they are clearly discernible from the galls of *Andricus kollari* forma *circulans*, the tops of which are rounded. The wall is very thin, its colour pale to greyish brown, the surface is more or less velvety-glossy. Most specimens have the same shade all over, with some the shade gets darker towards the top, see plate 3 fig. 4. The wasps gnaw a small, oval opening close below the top.

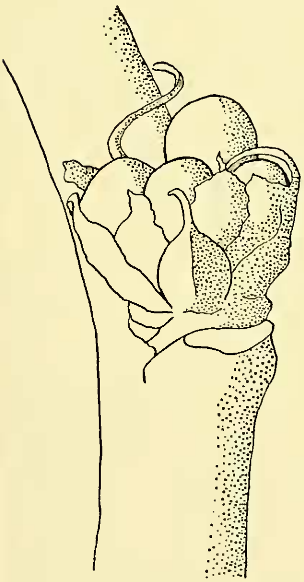


Fig. 1. Young, cultivated galls of *Andricus lignicolus* f. *vanheurni* nov. Amsterdam, February 21, 1957; × 12.

In 1955 these galls appeared in the first week of the month of May. The spring of 1957 was extremely mild and in that year the first gall was observed outside on the sleeved branches as early as April 12th. The not infected buds also began to come out. Therefore the gall can be said to come out at the same time as the budding leaves. The gall has a very rapid growth. On the first day the top of the gall can be seen between the receding bud-scales. Next morning half of the gall projects from between those bud-scales and soon after the wasp leaves its home, mostly between 8 and 10 a.m. Some wasps stay inside the gall for one or more days before coming out.

In his garden at Leersum the former author found the first gall on the sleeved branches on April 12th and during the next days he constantly noticed more of them, with 7 galls on April 17th. Altogether he collected 51 galls between April 12th and 29th; it may be that some galls escaped his notice.

The bigamic generation of *corruptrix* consists of dark, small wasps, which are extremely lively and which can fly very well. These wasps were named forma *larshemi*. While the wasps of the agamic generation are very quiet and immediately begin to lay eggs as soon as they have found a suitable bud of the Turkish oak, the bigamic wasps first have to copulate before they can proceed to deposit ova. When a male and a female wasp together are put in a glass tube they begin to copulate pretty soon. The copulation takes one minute or slightly shorter. The impregnated females then look for buds of *Quercus robur*. And now comes the difficulty. When the bigamic wasps come out the oak trees are budding. The trees are then found to have twigs with scarcely extended buds and others with developing young leaves. Therefore the wasps were sleeved on the twigs of three trees which in this respect represented various stages of development. Two of the trees displayed the early stages of developing leaves, the buds of the third one had only just begun to extend.

We put a great number — some 10 to 15 — of still closed galls in the bags which were sleeved on the twigs of these trees. After two weeks the sleeves were removed.

We did not find one single gall on the two trees of which the buds had already come out. But we found several galls on the specimen of which the buds had only just begun to extend. Two twigs turned out to have been infected, one bearing 4 galls, and one twig one gall of *corruptrix*. Thus the breeding experiment had been successful and it had proved that the new gall of *Quercus cerris* contains the bigamic generation of the *corruptrix* gall on *Quercus robur*.

Apart from Leersum this gall was also found on the Turkish oak near Wilp and near Wageningen.

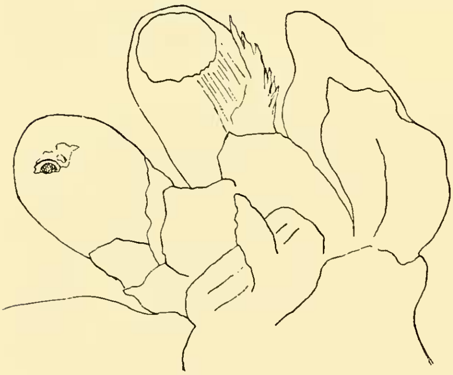


Fig. 2. Full grown, cultivated galls of *Andricus lignicolus* f. *vanheurni* nov.; in the left gall a wasp is gnawing a hole in the wall. Amsterdam, × 16.

THE LIFE-CYCLE OF *Andricus lignicolus*

The gall of the agamic generation has been known for quite a long time as occurring in middle and southern Europe. In the Netherlands it was found for the first time in the neighbourhood of Velp in 1942. Since then the gall has been collected in Wilp, Wageningen and Maastricht. Mr. VAN HEURN told us that in his country-seat at Wilp the galls are getting constantly more numerous; even the smallest oak shrubs are crowded with them. This will probably be due to the fact that the parasites and inquilines have not yet turned up or they are not yet very numerous. The first author experienced something of the same sort on a small scale in his garden at Leersum with the gall of *Andricus kollari.* In 1935 he planted a small Turkish oak in his garden and the next year he dropped some *kollari* galls at the foot of the tree. The year after that the gall was seen for the first time in the garden and during the next years it got gradually more numerous. The gall of the bigamic generation forma *circulans* was also found on the Turkish oak. During the first few years the *kollari* galls were found to be sound, undamaged and well developed, but gradually there also appeared smaller galls of a more irregular shape, containing inquilines. The *kollari* gall is still found in the garden at Leersum, but only in small numbers. Therefore it seems quite likely that the *lignicolus* galls will go back in number in the course of years, when inquilines and parasites make their appearance.

MAYR (1870, p. 16) mentions the *lignicolus* gall as being very common in the neighbourhood of Vienna and also in Hungary. We do not know anything about the occurence of the *kollari* and *lignicolus* galls in these regions now.

In 1954 Mr. VAN HEURN sent us material of the *lignicolus* galls from Wilp. The wasps appeared between July 6th and 18th. In 1956 Mr. VAN HEURN again sent us quite a number of galls. They were kept in cylindrical glass jars, the opening of which was shut off by means of netting. These jars were put outside on the north-facing window of a house in Amsterdam where the second author lived at the time. Between July 9th and 25th 22 wasps came out of those galls. Thus the wasps of the agamic generation of *lignicolus* may be said to appear in the month of July. The greatest number of wasps came forth on July 16th, that is 5 specimens. The graph 1 indicates on which days and in what numbers the wasps came forth.

In the Hortus Botanicus in Amsterdam there is a specimen of *Quercus cerris,* about 3 m tall. The *lignicolus* wasps were sleeved in large bags of netting round the branches of this tree. The bags were fixed horizontally and as the summer of 1956 was very rainy they were sheltered against the rain by a transparent plastic screen. Altogether 10 twigs about ½ m in length of this *cerris* tree were used in the experiment. After a fortnight the bags were removed.

The first galls of the bigamic generation appeared on February 21st.

They were found in the terminal and axillary buds of one year old twigs. Most buds contained more than

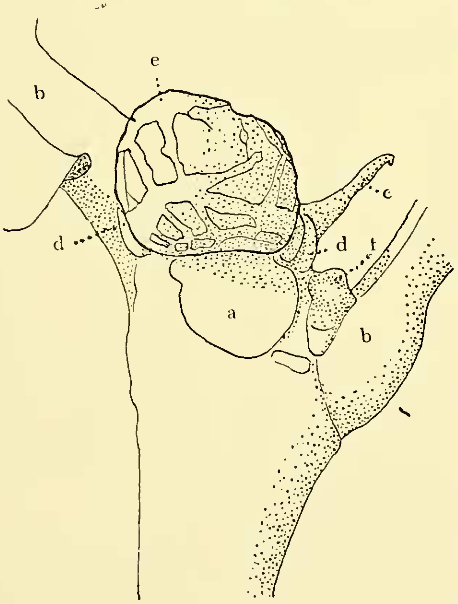


Fig. 3. Young, cultivated gall of *Andricus lignicolus,* Amsterdam, June 22nd 1957, × 10. a = broken off petiole; b = petiole; c = scale; d = stipule; e = epidermis; f = axillary bud.

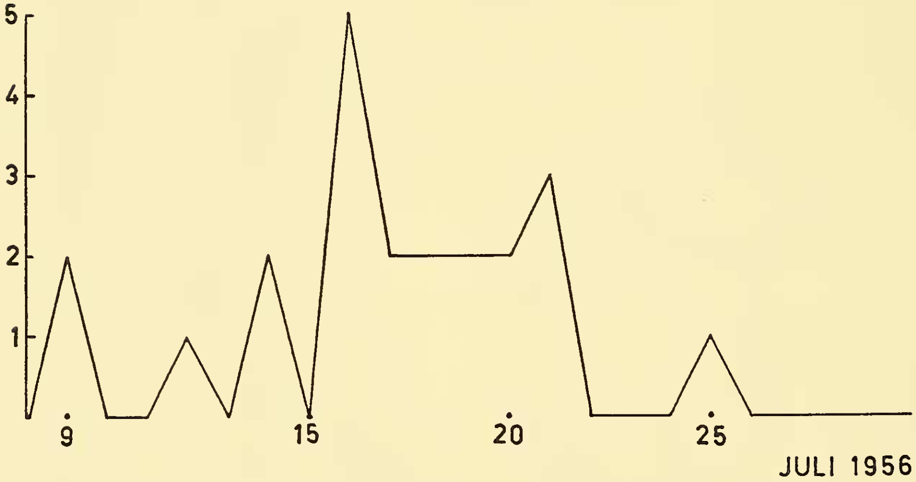
one gall, some up to 6 specimens. The form of the gall is oblong, the top is rounded, sometimes flattening towards the sides, when several galls are clustered together in a bud. The galls are velvety and purplish brown, greenish brown or yellowish brown and are quite similar to the *circulans* galls which contain the bigamic generation of *Andricus kollari.* Text figure 1 represents a cluster of young galls. Figs. 7 and 8 of plate 3 represent two twigs with galls. Some bud-scales have been removed in order to show the galls more completely; see also text figure 2.

As has been stated before these galls resemble the *circulans* galls; they may be just slightly smaller. Mayr (1870, p. 130) mentions a length of from 2 to 3 mm; Beijerinck (1897, p. 36) gives the same length and states that they measure 1½ mm across. Marsden-Jones gives as the greatest length 3 mm. The galls of the bigamic generation of *Andricus lignicolus* are about 2 mm long and 1½ mm across.

According to Mayr the colour of the *circulans* galls is brownish yellow, dirty red, brown or red. Beijerinck calls them yellow or yellowish white and Marsden-Jones describes the colour of the galls as Warm Buff tinged with Eugenia Red.

The wasps leave the galls through a round, lateral opening below the top, see plate 3 figs. 7 and 8. These wasps were called forma *vanheurni.*

The first *vanheurni* wasps came out on March 19th. That is slightly earlier than is stated about the *circulans* wasps. It may, however, have been due to the extremely warm spring of 1957, but it may just as well be a characteristic of the *vanheurni* wasps. For the *lignicolus* wasps also appear much earlier, about one month and a half, than the *kollari* wasps. Marsden-Jones states that the *circulans* wasps come out in April, May and early June.



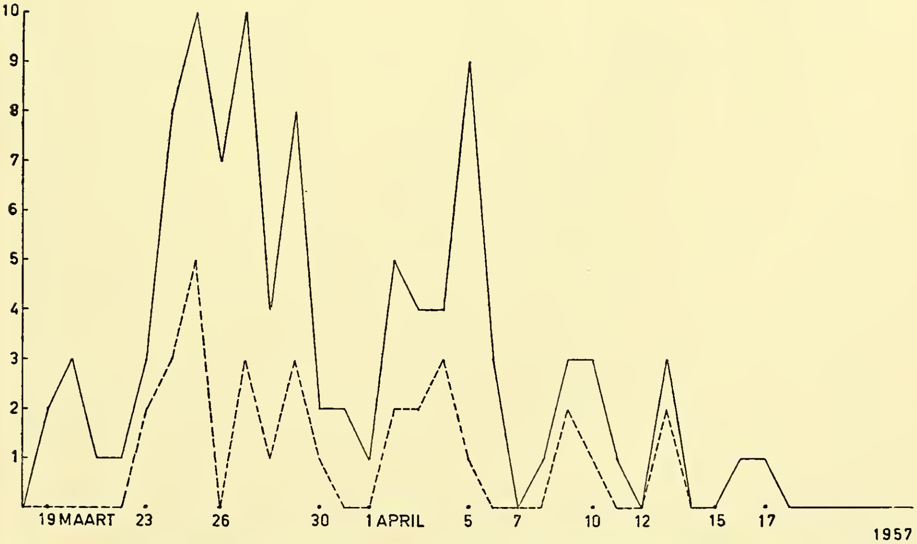
Graph 1. The wasps of *Andricus lignicolus* emerging from the galls.

It was the female wasps that came out first; the male *vanheurni* wasps appeared no earlier than March 23rd. The emergence of the wasps is charted in graph 2. The continuous line represents the number of wasps appearing each day, the dotted line the same data of the male insects only. The last wasp, a female came out on April 17th.

Between March 19th and April 17th 67 ♀ and 33 ♂ wasps in all came out. The wasps emerge from the galls early in the morning, almost all of them before 10 a.m. When a male and a female are put together in a glass jar they begin to copulate immediately. This takes from ½ to 1 minute. MARSDEN-JONES (1953, p. 219) writes that the *circulans* wasps soon begin to copulate. This is in contrast with BEIJERINCK's (1902, p. 17) statement that he did not see the wasps copulate. Neither did BEIJERINCK observe the females depositing eggs in the buds of *Quercus robur*. NIBLETT (1953—54, p. 143) and MARSDEN-JONES were more successful; BEIJERINCK explains why his infection experiments were not successful by the fact that the wasps are good flyers and that at first they must fly about for some time before they begin to copulate. His opinion, however, is rectified by what has been observed in the last few years.

For the breeding experiments of the *vanheurni* wasps we chose a tree of *Quercus robur* about 2 m high and also 4 specimens three years old. The latter were sleeved entirely. Of the former specimen 4 branches, about ½ m long were used. As the days on which the experiments were taken were extremely wet we put up a shelter of transparent plastic.

The small *vanheurni* wasps were still alive after the course of 6 days, but for the greater part they sat against the walls of the sleeves. Just as in case of the *larshemi* galls wasps too will only then start to deposit their eggs when the buds are in exactly the right stage of development. But although the greater part of the sleeved wasps did not lay any eggs the result was still quite satisfactory. On June 22th the 2 m high oak bore the first *lignicolus* galls. There were 8 galls in all.



Graph 2. The emergence of the wasps of *Andricus lignicolus* forma *vanheurni* nov. from the galls. Continuous line: all wasps; dotted line: male wasps.

The young *lignicolus* galls are grey with dark brown areas, see text figure 3. These discolourings are the remainders of the burst epidermis of the gall which has only partly fallen off. In the end only irregular lines of the epidermis remain. In this respect the *lignicolus* gall differs from the gall of *Andricus kollari.* The latter drops the epidermis completely so that the surface is smooth. On maturity the remainders of the epidermis give the *lignicolus* gall a rough appearance and an irregular surface, so that apart from its size it can be easily discerned from the *kollari* gall. There are instances where the epidermis of the *lignicolus* gall also disappears completely. In those cases it is the situation of the gall-chamber which distinguishes one from the other, see the previous article.

BEIJERINCK (1882, p. 150) demonstrated that the *kollari* gall does not develop from the bud, but by its side. It may be said that the same thing happens in case of the *lignicolus* gall. The bud is clasped between the gall and the twig. Figure 3 represents a very young gall many times its natural size. The explanation of the letters will be found under the picture. The shape of the young gall is irregularly round, the width is greater then the height. This gall was drawn on June 22th. On July 19th, that is about a month later, the galls were full-grown and measured 7 to 10 mm across. The cultivated galls are represented on plate 3 figs. 5 and 6. The galls remain attached to the twig all through the winter and the wasps come forth in the month of July of the second year. A few wasps come forth still a year later and it may be that others take even longer.

DISCUSSION

The bigamic generations of *Andricus kollari* and *lignicolus* develop in identical bud-galls on *Quercus cerris*, the only difference being that the *kollari* galls are slightly bigger and come out at a slightly later time.

MAYR (1870, p. 30) bred *Andricus circulans* on the Turkish oak from bud-galls which he had collected in the surroundings of Vienna. The difficulty is, however, that we do not know which wasp was described by MAYR. We cannot be sure whether the *circulans* wasps described by him were bred from galls of the bigamic generation of *kollari*, of *lignicolus* or a combination of these two. Besides there is a chance that other gall-wasps cause galls on the common oak, the bigamic generations of which live in such bud-galls on *Quercus cerris.* We are thinking of *Andricus conglomeratus*, the galls of which are very similar to those of *kollari* and *lignicolus.* This should be verified by breeding experiments, but the possibility exists. There are still other galls which resemble *kollari* galls, for instance *tinctoria*, *argentea* and *hungarica.* From which of these wasps can the *circulans* wasp described by MAYR form the bigamic generation ?

At the end of last century when BEIJERINCK discovered heteroecism with *Andricus kollari*, this *kollari* was the only one of the above mentioned species which occurred in the Netherlands. Therefore the wasps of the bigamic generation as bred by BEIJERINCK undoubtedly belonged to this gall-wasp. Consequently it seems most simple to keep the name forma *circulans* for the bigamic generation of *kollari.* We failed to find any material of the wasps bred by BEIJERINCK in the collection bequeathed by him.

In the garden of the first author at Leersum *kollari* galls have been collected, but no *lignicolus* galls. Therefore the bud-galls on *Quercus cerris* could only contain the wasps of forma *circulans*. Two of them, one ♀ and one ♂ were raised and preserved in 1957.

Actually *Andricus corruptrix, kollari* and *lignicolus* can only be distinguished from one another by the galls of the agamic generation; only the gall of forma *larshemi* is different from those of *circulans* and *vanheurni*. In the case of gall-wasps there are more examples of species which can only be distinguished mutually by their galls. Let us mention a few.

Trigonaspis megaptera forma *renum* and *T. synaspis*, both agamic generations cause galls of very different shapes. The *renum* galls are small, kidney-shaped light coloured leaf-galls, which appear in the autumn. The *synaspis* galls are big, round, and green with red lines or dots, while they appear early in the summer. The two wasps are very similar, they are not winged, the *synaspis* wasp, however, is slightly bigger than the *renum* wasp. Besides, the former species shows distinctly bidentate tarsal claws, while the second species shows indistinctly bidentate ones. The wasps of the bigamic generations *megaptera* and *synaspis* forma *megapteropsis* cannot be distinguished and neither can their galls which appear early in spring.

The galls of the agamic *Cynips divisa* and *disticha* can easily be told apart, but this can hardly be said about the wasps. The wasps and the galls of the bigamic generation are completely identical, see DOCTERS VAN LEEUWEN (1947, p. 271) and NIBLETT (1948, p. 143). The difference of the two species lies again in the different shapes of the galls caused by the wasps of the agamic generations.

Similar phenomena can be found in case of other gall-causers. Five species of aphids of the genus *Sappaphis* cause the same pouch-like red leaf-gall on the leaves of *Crataegus*. The aphids are discernible from one another because each species moves to a different host-plant belonging to the Compositae. Therefore they can best be sorted by breeding them and checking to what host-plant they move.

Also in case of the fungi such cases are observed. *Uromyces dactylidis* and *poae* cause identical leaf-galls on species of *Ranunculus*. These two species can only be discerned when they are bred further and it is seen that the former species moves to *Dactylis glomerata* and the second to species of *Poa*.

These phenomena have of course not escaped the notice of other research-workers. KINSEY (1929, p. 91) writes: "All the Central European insects of *Cynips*, both in their agamic and bigamic generations are strikingly alike altho their galls are distinct enough. The group thus offers a good example of physiological species i.e. species in which physiological matter (the gall-producing capacity) has mutated faster than any of the morphological characteristics of the insects". We still know too little about the causes of gall-production to feel justified to use the word mutation, but the phenomenon by itself is already extremely interesting.

MARSDEN-JONES (1953, p. 197) writes in his profound treatment of the subject: "BEIJERINCK's experiments with *Adleria kollari* are of great interest". In our opinion this is an understatement. Without the discovery of heteroecism of *Andricus kollari* nobody would have doubted whether this gall-wasp only occurs in the agamic generation. BEIJERINCK (1882, p. 139) himself writes that he has shown this by breeding experiments. ADLER (1882, p. 201) has demonstrated some other instances of such-gall-wasps which only occur in an agamic generation, i.e., *Andricus albopunctatus, marginalis, quadrilineatus* and *seminationis*. (We wonder, however, whether careful breeding experiments would not yield surprising results).

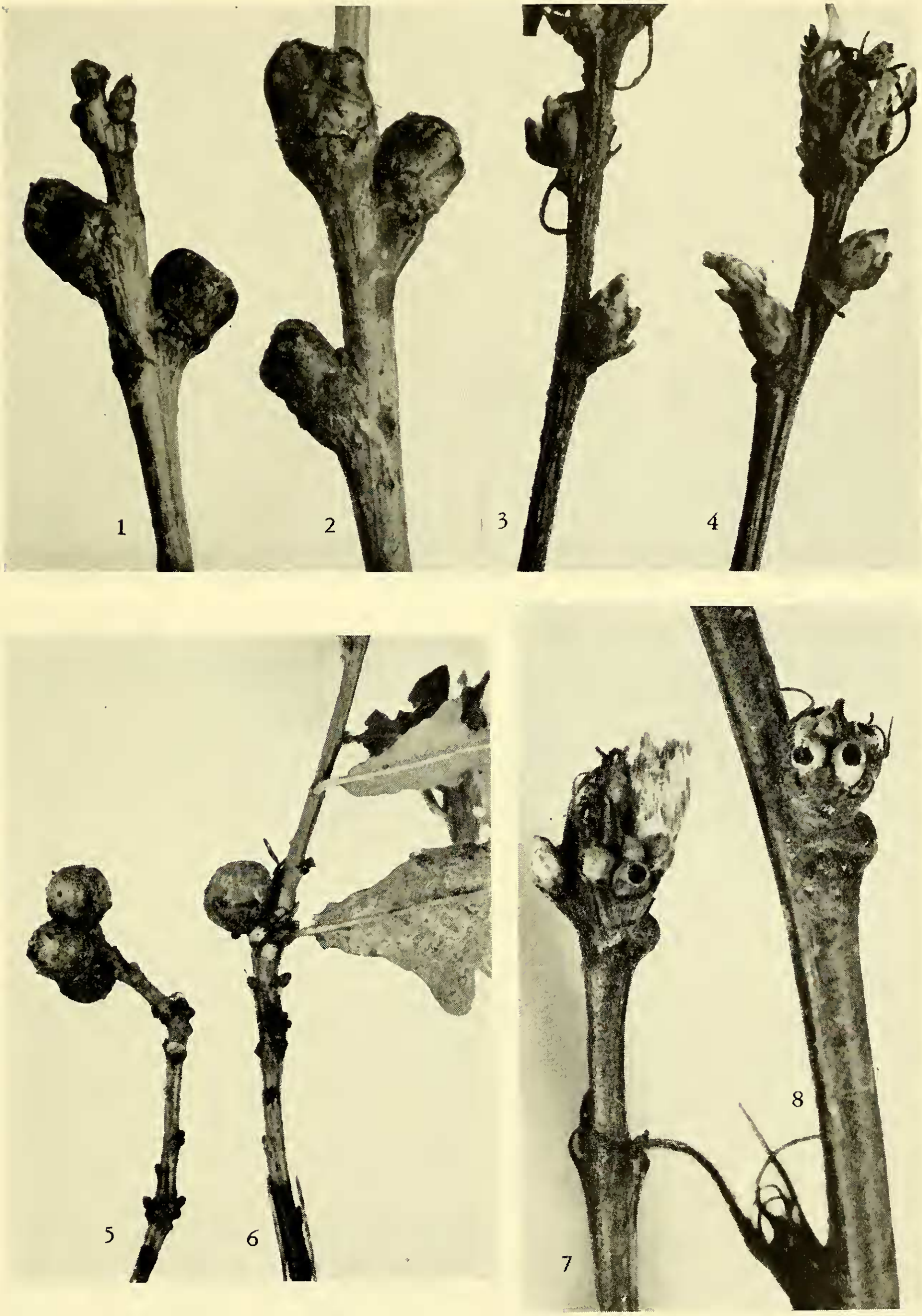
BEIJERINCK has not taken sufficient precautionary measures at the time of his experiments with the *kollari* wasps, because 20 years later he discovered alternation of generations and heteroecism of this wasp. The discovery by this Dutch biologist of surprising endowments was not merely interesting but fundamental and broke new ground. It opened up new ways and possibilities. BEIJERINCK realized this when a short time before he had discovered the alternating of generations and heteroecism of *Andricus calicis*.

As often happens with such unexpected discoveries nobody could bring himself to believe it. GUSTAV MAYR, the well-known Austrian student in the field of Hymenoptera wrote to the first author in 1905 that he did not attach any importance to BEIJERINCK's work. RIEDEL (1910, p. 55) writes in his description of *Andricus calicis*: "At this point I want to refer to the curious alternation of generations as mentioned by BEIJERINCK in his article: "Ueber Gallbildung und Generationswechsel bei *Cynips calicis*". According to BEIJERINCK the agamic *Cynips calicis* wasp of the common oak is an alternating generation of the wasp of *Quercus cerris*, the bigamic *Andricus cerri*. So far this is an isolated piece of news, firstly that there is alternating of generations with a species of *Cynips* and secondly that wasps living on *Quercus robur* deposit their eggs on *Quercus cerris* and the other way about, that wasps living on *Quercus cerris* should deposit their eggs on *Quercus robur*". Eight years after BEIJERINCK published his article in *Marcellia* RIEDEL does not mention it in his discussion of the *kollari* gall. In other words, RIEDEL did not believe BEIJERINCK's statements in the least.

It was only 50 years after BEIJERINCK's publication that NIBLETT and MARSDEN-JONES confirmed by means of breeding experiments that BEIJERINCK was right.

When we started our research of the alternating generations of *Andricus corruptrix* and *lignicolus*, the galls of which have been found in the Netherlands only lately, we expected that we should have to look for the bigamic generations of these gall-wasps in galls on *Quercus cerris*. The question therefore was quite simple, because we knew how to direct our quest. We were fevoured by the fact that our breeding experiments yielded such quick and complete success.

BEIJERINCK was the pioneer in other fields of science too. He opened up the road for others who follow in his track more or less successfully.



Figs. 1 and 2. Galls of *Andricus corruptrix*, × 3. 3 and 4. Galls of *Andricus corruptrix* forma *larshemi* nova, × 3. 5 and 6. Galls of *Andricus lignicolus*, × 1. 7 and 8. Galls of *Andricus lignicolus* forma *vanheurni* nova, × 3

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